



## Nutrient optimization of tree growth alters structure and function of boreal soil food webs

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### ABSTRACT

Nutrient optimization has been proposed as a way to increase boreal forest production, and involves chronic additions of liquid fertilizer with amounts of micro- and macro-nutrients adjusted annually to match tree nutritional requirements. We used a short-term (maintained since 2007) and a long-term (maintained since 1987) fertilization experiment in northern Sweden, in order to understand nutrient optimization effects on soil microbiota and mesofauna, and to explore the relationships between plant litter and microbial elemental stoichiometry. Soil microbes, soil fauna, and aboveground litter were collected from the control plots, and short- and long-term nutrient optimization plots. Correlation analyses revealed no relationships between microbial biomass and litter nutrient ratios. Litter C:N, C:P and N:P ratios declined in response to both optimization treatments; while only microbial C:P ratios declined in response to long-term nutrient optimization. Further, we found that both short- and long-term optimization treatments decreased total microbial, fungal, and bacterial PLFA biomass and shifted the microbial community structure towards a lower fungi:bacterial ratio. In contrast, abundances of most fungal- and bacterial-feeding soil biota were little affected by the nutrient optimization treatments. However, abundance of hemi-edaphic Collembola declined in response to the long-term nutrient optimization treatment. The relative abundances (%) of fungal-feeding and plant-feeding nematodes, respectively, declined and increased in response to both short-term and long-term treatments; bacterial-feeding nematodes increased relative to fungal feeders. Overall, our results demonstrate that long-term nutrient optimization aiming to increase forest production decreases litter C:N, C:P and N:P ratios, microbial C:P ratios and fungal biomass, whereas higher trophic levels are less affected.

### 1. Introduction

Boreal forest growth is generally limited by nitrogen (N), while limitation by other nutrients such as phosphorus (P) and potassium (K) become increasingly important when N is supplied (Tamm, 1991; Tanner et al., 1998; Tripler et al., 2006). In order to enhance timber production and increase carbon (C) sequestration, alleviating nutrient limitation in boreal forests is common (Beringer et al., 2011; Fernández-Martínez et al., 2014). In general, increased nutrient availability via fertilization enhances photosynthetic rate, foliar nutrient content, and tree growth and C accumulation (Bergh et al., 1999; From

et al., 2016; Niu et al., 2016). In Scandinavian forestry, fertilizers are commonly applied as a single dose or as repeated applications of solid N fertilizer (ca. 150 kg N ha<sup>-1</sup>) (Bergh et al., 2005; From et al., 2015). However, solid N fertilization can also have detrimental effects on boreal forest ecosystems, such as compositional shifts in understory vegetation, nutrient imbalances, nutrient toxicity effects, nutrient leaching, as well as shifts in soil community structure and functioning (Binkley and Högberg, 2016; Gundale et al., 2011; Lucas et al., 2011; Strengbom and Nordin, 2008; Treseder, 2008).

As an alternative to solid N fertilization, the nutrient optimization approach entails the chronic addition of liquid fertilizer containing

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micro- (Mn, Fe, Zn, Cu, B and Mo) and macro-nutrients (N, P, K, Ca, S and Mg) through an irrigation system. This may reduce some of the detrimental effects mentioned above for N fertilization (e.g. Fransson et al., 2000). So far, most nutrient optimization studies in boreal ecosystems have focused on aboveground organisms, reporting a decline of understory vegetation of the most common plant groups, i.e. bryophytes and ericaceous dwarf shrubs (Hedwall et al., 2013; Strengbom et al., 2011). Changes in understory vegetation may in turn affect the structure and functioning of aboveground food webs, specifically herbivores and herbivore-predator interactions (Meunier et al., 2015; Throop and Lerdau, 2004). Despite plant litter serving as primary C resource for soil decomposers, few studies have investigated how nutrient optimization impacts litter-mediated effects on soil biota and their trophic interactions (Lindberg and Persson, 2004).

In addition to changing the quantity or quality of organic inputs (e.g. plant litter, mycorrhizal C transfer, and root exudates), fertilization may also alter the chemistry of organic matter, that subsequently impacts the activity and community structure of primary consumers (i.e. microbes; Bokhorst et al., 2017; Meunier et al., 2015; Wallenda and Kottke, 1998). For example, Maaroufi et al. (2015) reported a decline of fungal biomass in forest plots where half of the total N added over 16 years of N fertilization was retained in the soil humus, thereby reducing the humus C:N ratio. Similar patterns have been reported in other nutrient optimization studies (Demoling et al., 2008; Fransson et al., 2000). While these studies demonstrate impacts of nutrient enrichment on soil microbial biomass, nutrient enrichment may also impact microbial C:N:P stoichiometry. This is of great interest because changes in microbial elemental stoichiometry may control key soil processes such as nutrient retention and losses (Zechmeister-Boltenstern et al., 2015). It has been proposed that globally the C:N:P stoichiometry of microbial communities is very stable and independent of the environmental nutrient availability (Cleveland and Liptzin, 2007;

Mooshammer et al., 2014). However, other studies have challenged this view by showing that microbial community C:N:P stoichiometry can vary with its surrounding environment (e.g. soil and soluble litter fractions) (Fanin et al., 2013; Tischer et al., 2014). Thus, it remains poorly understood to what degree nutrient optimization affects soil microbial stoichiometry.

Changes in microbial abundance and stoichiometry may further affect soil fauna at higher trophic levels of the soil food web (see Fig. 1). Soil fauna are of interest because they regulate ecosystem processes involved in organic matter turnover and associated nutrient mineralization (Bardgett and Wardle, 2010). Soil organisms may respond positively or negatively to nutrient addition in forest ecosystems. For example, long-term N addition studies have shown a decline of fungal-feeding and predaceous soil fauna in northern and sub-alpine forests (Gan et al., 2013; Xu et al., 2009). The few nutrient optimization studies focusing on soil food webs have also shown mixed effects on soil fauna. For example, after 10 years of nutrient optimization, Berch et al. (2009) did not find any effects on fungal-feeding Collembola but an increase of fungal-feeding mites. In contrast, Lindberg and Persson (2004) found no impact on fungal-feeding mites but an increase of Collembola after 12 years of nutrient optimization. In boreal forests, the main decomposition pathway is generally fungal-based, consisting of fungal biomass, fungivores and their predators. Previous studies have reported a decline of fungal decomposers and their activity in response to N fertilization relative to bacteria (Treseder, 2008). Thus, the relative importance of fungal versus bacterial decomposition pathways (also referred to as energy channels) might be also altered by nutrient optimization.

Here, we made use of a long-term fertilization experiment, maintained since 1987 at Flakaliden in northern Sweden, to characterize the ecological consequences of nutrient optimization on soil biota. Specifically, we studied the effect of short-term (6 years) and long-term

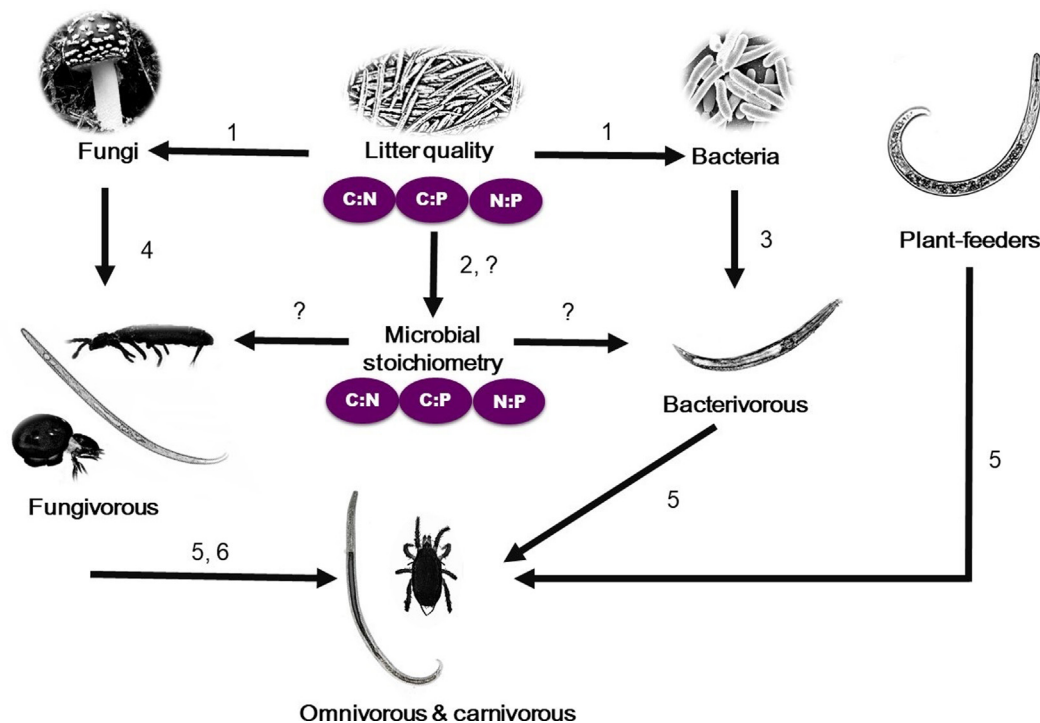


Fig. 1. Conceptual model showing the potential effects of litter and microbial elemental stoichiometry on soil food webs. Arrow numbers indicate different pathways and their associated mechanisms. Question marks indicate unknown or not well established relationships that were tested in this study. Litter quality may influence the primary consumers (bacteria and fungi) as aboveground litter represents one of the basal resources for the microbiota (1) (Coleman et al., 2004); litter quality may influence microbial stoichiometry (2; ?) (Tischer et al., 2014); bacteria are the primary food resource of bacterial-feeding nematodes (3) (Yeates et al., 1993); fungi are the primary food resource of fungal-feeding mites, fungal-feeding nematodes and Collembola (4) (Chahartaghi et al., 2005; Coleman et al., 2004; Yeates et al., 1993); nematodes are food resources for omnivorous and carnivorous nematodes (5) (Yeates et al., 1993); fungal-feeding mites, Collembola and nematodes are food resources for predatory mites (6) (Klamer et al., 2013).

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